

Reproduction: The Adaptive Significance of Endothermy

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A central theme raised by Angilletta and Sears is that the energetic cost of endothermy is too enormous to be offset by the benefits that thermogenesis could provide for reproduction. Angilletta and Sears suggest that parents would have been better off producing additional offspring with the energy used for incubation or minimizing their risk of predation by minimizing foraging efforts. However, these views overlook the fact that a defining characteristic of both birds and mammals is high investment in relatively few offspring. The evolution of parental provisioning behaviors is cogent evidence that minimizing foraging efforts and risks of adult predation were not favored over energy expenditure for parental care. Furthermore, the energetic costs of parental feeding of offspring demonstrate that the benefits of parental care can outweigh energetic expenses that exceed by far the cost of endothermy. If the great energetic expense of parental feeding has been favored evolutionarily, it is reasonable to propose that the lesser cost of thermogenesis could be favored for the same reproductive benefit.

For example, thermoregulation is expensive for house mice because they are small (26–44 g), but thermoregulatory costs are not nearly as large as the cost of feeding offspring. When living at 21°C, house mice consume approximately 25-fold more food than lava lizards of similar mass living in the field (82.92 and 3.37 kJ d⁻¹, respectively); when exposed to cold (8°C), the mice consume 38-fold more food (126.8 kJ d⁻¹) than the lizards. Although these energetic costs seem enormous, they are dwarfed by the energetic expense of parental feeding. At peak lactation,

mice living at 21°C need approximately 4.4-fold more food than nonreproductive females (369.6 kJ d⁻¹), which is 110-fold more food each day than lava lizards need (Johnson and Speakman 2001; Johnson et al. 2001; Nagy 2001). Lactation is the most energy-expensive period for many other mammals as well (reviewed in Hammond and Diamond 1997). For example, daily energy expenditure (DEE; often referred to as field metabolic rate [FMR] when measured in the field on free-living animals) during lactation in gray seals is 7.4-fold the resting metabolism (Mellish et al. 2000).

When provisioning young, birds also increase DEE up to 6.6-fold their resting metabolism (reviewed in Hammond and Diamond 1997) and elevate FMR two- to five-fold over nonreproductive birds (Walsberg 1983; Weathers and Sullivan 1989; Peterson et al. 1990; Hodum and Weathers 2003), but these numbers do not represent the total energy investment of parental feeding. Because DEE reflects rates of food assimilation (and carbon dioxide production), the elevated DEE (FMR) of lactating mammals includes both the food ingested by the mother and converted to milk and the food eaten to support expanded foraging efforts. In contrast, the increase in DEE (FMR) of parental birds only represents the extra food eaten by the parent to support expanded foraging. To this energy budget one must add the food brought to the offspring (carried unassimilated in the beak, talons, crop). Because chicks often grow very fast, this energy requirement can be large (Weathers 1992). Furthermore, because in many avian species both parents provide food to the young, the total energy needed for parental provisioning of offspring is the sum of the energy obtained by the two parents. All told, parental feeding in birds can therefore carry an enormous energetic cost. Of course, the cost of thermoregulation varies with body size, thermal conductance, and the temperature gradient being maintained (Webster and Weathers 2000; Piersma et al. 2003). Nevertheless, the energetic costs of providing food to young in both the avian and mammalian lineages can exceed and even dwarf the energetic expense of endothermy (reviewed in Hammond and Diamond 1997).

A major advantage of parental feeding of young is contraction of the period of time between conception and

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sexual maturity through increased growth rates of juveniles (Pond 1977, 1983). Given that parental provisioning of food to offspring with its very high energetic cost has been favored among birds and mammals, it is reasonable to suggest that parental provisioning of heat to offspring, with its lower cost, could also have been selected for the same reproductive benefit. Clearly, the evolution of parental provisioning indicates that minimizing foraging efforts, minimizing risks of adult predation, and minimization of daily energy expenditures were not favored over energy expenditure to reduce developmental time in the avian and mammalian lineages.

Ample Evidence of Fitness Benefits of Embryo Incubation

Angilletta and Sears suggest that reptilian developmental data provide mixed evidence for the hypothesis that parental control of incubation temperature can be adaptive. Although I agree with Angilletta and Sears that the effects of temperature on development depend on the frequency, amplitude, and waveforms of the thermal regime and that the effects can vary among different lineages of animals, I disagree with their suggestion that these complexities weaken the evidence for strong selective benefits to control of incubation temperature. The extraordinary convergent evolution of this trait is a robust line of evidence that it is adaptive. Because parental control of incubation temperature is remarkably widespread among distantly related groups and involves many similar but complex innovations, the possibility that it is a "spandrel" (Gould and Lewontin 1979) is remote. For example, retention of embryos in utero (viviparity, ovoviviparity) has arisen independently an extraordinary number of times, at least 100 times in 20 different families of reptiles alone; a major selective advantage for the evolution of this trait is that the mother can better control incubation temperature by retaining the embryos than if she deposited the eggs (Guillette et al. 1980, 1982; Blackburn 1982; Shine 1983, 1985, 1988, 1989, 1991; Greene 1997; Qualls 1997; Qualls and Andrews 1999). In contrast to these very small squamate reptiles that rely on behavioral thermoregulation, in some large viviparous and ovoviviparous sharks, uterine temperatures are controlled with metabolically produced heat by elaborate retia mirabilia that enable endothermy (Carney et al. 1981; Fudge and Stevens 1996). Viviparity is an adaptation for parental care and is but one stunning example of convergent evolution that serves this function.

Within the class Insecta (especially among the Hymenoptera and Isoptera) as well as among vertebrates, the following behavioral, morphological, and physiological innovations that enable control of incubation temperature have evolved repeatedly (see Farmer 2000 for references):

the practice of constructing elaborate nests with carefully guarded temperatures of nursery chambers (e.g., termites, ants, bees and wasps, crocodilians and other nonavian reptiles, birds, and mammals), the behavior of huddling (e.g., army ants, bees, caterpillars, rodents, penguins), manipulation of offspring location (ants, many lizards), solar basking of an adult that returns to a nest to warm eggs (many snakes and lizards), body insulation (e.g., the setae of caterpillars, the pile of bumblebees, mammalian hair, feathers), brood patches (bees, birds), and thermogenesis. Control of incubation temperature with thermogenesis has evolved in sharks (perhaps several times), crocodilians (the heat is produced by bacteria in the decomposition of organic materials used in the nest), pythons, birds, and mammals, and it is thought to have evolved independently in both sister groups of bees, the phylogenetically ancient Apinae and the Meliponidae (Engels et al. 1995). Like vertebrates, some bees have highly evolved thermoregulatory and thermogenic abilities. For example, when colonies of honeybees contain eggs, larvae, and pupae, thermogenesis is used to maintain brood nest temperature at 32–36°C, even when ambient temperature drops as low as –30°C or less. The energetic cost of brooding for a bee is thought to be about the same as the cost of flight (reviewed in Seeley and Heinrich 1981). Impressive thermogenic and thermoregulatory abilities are also found in vespine wasps (yellow jackets and hornets). When brooding, a queen wasp (*Dolichovespula arenaria*) can generate >120 cal/h. To maintain this level of heat production, the queen must metabolize each hour a mass of nectar that is approximately 30% of her body mass (reviewed in Seeley and Heinrich 1981). Even thermogenesis in protozoa (e.g., *Euglena gracilis*) and plants (thermogenesis evolved independently several times, e.g., members of the Araceae and the lotus) is thought to primarily benefit reproduction (Heinrich and Cook 1967; Nagy et al. 1972; Heinrich 1977; Seymour and Schultze-Motel 1996; reviewed in Seymour 1997).

Thus, Angilletta and Sears's concerns about exactly how the variance and mean of thermal regimes affect development and growth in individual lineages of squamate reptiles can be laid to rest by this extraordinary convergent evolution. The fact that many behavioral, morphological, and physiological characters enabling control of developmental temperatures have evolved repeatedly in the same context gives credence to the hypothesis that reproductive benefits were a principal factor in the evolution of vertebrate endothermy.

Angilletta and Sears suggest that data on the thermal limits of avian embryos do not provide support for the parental care scenario because there is no way to identify whether these limits are the cause or effect of care by an endothermic parent. However, patterns of evolutionary

change can be deduced using phylogenetic knowledge. Crocodylians are the other extant group of archosaurs and are ectothermic. Because the embryos of crocodylians have narrow thermal tolerances, it is parsimonious to map this character to the base of Archosauria. Angilletta and Sears also suggest that the majority of studies on the effects of temperature on development of nonavian reptiles are irrelevant because they were conducted at constant temperatures. Dismissal of this wealth of information eliminates prudent interpretation of the available data.

Furthermore, I find no evidence that the studies they cite offer only mixed support for the parental care hypothesis. On the contrary, the studies provide strong support by showing one or more of the following effects of temperature on development: modification of phenotype (Georges et al. 1994; Castilla and Swallow 1996; Qualls and Shine 1996, 1998, 2000; Shine and Harlow 1996; Elphick and Shine 1998; Qualls and Andrews 1999; Shine 1999; Andrews et al. 2000), change in incubation period (Christian et al. 1986; Castilla and Swallow 1996; Qualls and Shine 1996, 1998, 2000; Shine and Harlow 1996; Elphick and Shine 1998; Qualls and Andrews 1999; Shine 1999; Andrews et al. 2000), effects on hatching success (Christian et al. 1986; Qualls and Shine 1996; Qualls and Andrews 1999; Andrews et al. 2000), and effects on survival of the hatchlings (Qualls and Shine 1996; Elphick and Shine 1998; Qualls and Andrews 1999; Andrews et al. 2000).

In scrutinizing the literature, Angilletta and Sears have overlooked numerous important facets that are relevant. For example, it is true, as Angilletta and Sears noted, that a 5-d exposure to cold was not lethal to *Sceloporus* lizards, but this was only when the embryos were maintained under diel cycles of temperatures with highs of 29° and 30°C (Andrews et al. 2000). When embryos experienced diel cycles of temperatures with peaks that were 4°–5°C lower (diel 15°–25°C), the 5-d exposure to cold increased mortality from 15% to 41% (Andrews et al. 2000). Similarly, Christian et al. (1986) found no mortality in *Sceloporus* with 4 d of exposure to cold (the embryos were otherwise held at 30°C); however, Christian et al. (1986) also report 50% mortality at 9 d (Christian et al. 1986). Furthermore, an acute exposure to cold may have no effect during one stage of development but be lethal if experienced during a critical period (reviewed in Deeming and Ferguson 1991). Although Angilletta and Sears are correct in that daily exposure to cold does not necessarily cause mortality of eggs even though a constant exposure to that temperature would be lethal, the converse is also true; daily exposure to warm temperatures has been shown to enhance development even though chronic exposure to that temperature would be lethal (Andrews and Rose 1994; Shine and Harlow 1996; Angilletta et al. 2000). Furthermore,

temperature can affect fitness in numerous and complex ways such as energy-use patterns during development and the growth rates of juveniles (reviewed in Deeming and Ferguson 1991), heterochrony (McKinney and McNamara 1991), developmental instability (Qualls and Andrews 1999), and cross-generational effects (Gilchrist and Huey 2001).

The scrutiny by Angilletta and Sears also overlooked the fact that development and growth are more sensitive to temperature than other aspects of reptilian physiology such as locomotion (Deeming and Ferguson 1991; Angilletta et al. 2002). For example, lizards typically maintain sprint speeds within 80% of the maximum at body temperatures (T_b) that span 10°–20°C (Angilletta et al. 2002), and some heterothermic birds and mammals allow T_b to fluctuate over 10°–14°C with no ill effect on the state of alertness or locomotor performances (Merola-Zwartjes and Ligon 2000; Wooden and Walsberg 2002, 2003). In contrast, temperature differences of several degrees often have large effects on development. For example, when embryos of the lizard *Sceloporus undulatus* were incubated at 30°C compared with 28°C, Angilletta et al. (2000) reported improved hatching success (86% compared with 62%), a decrease in the incubation period (48 d compared with 55 d), and improvements in energy use patterns (both temperatures are well within the thermal tolerance of this species). Similarly, a difference of only 3°C has a major impact on development of the python *Liasis fuscus* (Shine et al. 1997b). A diel fluctuation from 27° to 33°C, compared with 24° to 33°C, shortens the incubation period from 80 to 68 d, increases the growth rate of the hatchlings, and affects body shape and behavior. These temperature gradients do not present insurmountable cost barriers; field studies demonstrate that female pythons can afford to maintain brood temperature as much as 9°–13°C above ambient temperature (Slip and Shine 1988). A temperature change of 9°C is large enough to significantly influence development in every group of reptiles of which I am aware (Deeming and Ferguson 1991; Georges et al. 1994; Castilla and Swallow 1996; Qualls and Shine 1996; Shine and Harlow 1996; Andrews et al. 1997, 2000; Shine et al. 1997a, 1997b; Elphick and Shine 1998; O'Steen 1998; Angilletta et al. 2000).

If one looks broadly at the data, a reasonable conclusion is that temperature is quite important to development in a number of different ways. The idea that manipulation of incubation temperature through thermogenesis could be adaptive and affordable is well supported by these studies on the effects of temperature on developing reptiles and by the remarkable convergent evolution of this character.

Additional Questions about the Hypothesis

Why Homeothermy?

The basis of this hypothesis is that the selective benefits of endothermy are primarily reproductive. Selection for faster rates of juvenile growth could have extended the time adults expressed endothermy beyond the period of embryo incubation to include incubation of juveniles. Contingent upon adequate food, water, and oxygen supplies, in a broad range of extant vertebrates and invertebrates, warmer temperatures (within the viable range) produce more rapid rates of growth for both embryos and juveniles (Pond 1977; Savory and MacLeod 1980; Heinrich 1981; Buffenstein and Louw 1982; Williamson et al. 1989; Deeming and Ferguson 1991; Ferguson and Talent 1993; Autumn and DeNardo 1995; Kingsolver and Woods 1997; Blouin and Brown 2000; Gillooly and Dodson 2000*a*, 2000*b*; Gilchrist and Huey 2001; Angilletta et al. 2002; Gillooly et al. 2002). Because parental provisioning of heat could have sped growth just as parental provisioning of food does, selection on the parent for thermogenesis would have extended well beyond hatching or birth. Similarly, selection for thermogenesis in the juveniles themselves could have been favored if their heat was retained so that it could facilitate growth, for example, if the juveniles huddled in an insulated nest (consider the impressive thermogenic abilities that have evolved in larval vespine wasps [reviewed in Seeley and Heinrich 1981]), were of large body size, or had evolved insulation. Thus the transition toward homeothermic endothermy could have resulted from a gradual extension of the same selective pressures acting on both offspring and adult. A strength of this hypothesis is that mechanistic information on the effects of temperature on reproduction fits with historical information; exceptionally high rates of growth are thought to have been present among both ornithosuchians and the rapsids (de Ricqlès 1974; Padian et al. 2001).

This scenario is distinct from other hypotheses for the evolution of endothermy in that it proposes that the initial and primary selective benefits of thermogenesis were reproductive (rather than relating to locomotor performance). However, in lineages where the energetic costs of thermogenesis were balanced by resource availability, non-reproductive benefits of homeothermy may have been found in a general stability of protein structure and improvements in catalytic rates of enzyme systems (Heinrich 1977; Crompton et al. 1978; McNab 1978). Thermal stability appears to be especially important for the central nervous system (discussed in Block and Finnerty 1994). Thus although the initial selective benefits of thermogenesis are proposed to have been for reproduction *per se*, nonreproductive benefits could have subsequently contributed to the evolution of homeothermic endothermy.

Why Not Heterothermy?

If the reproductive hypothesis is correct, Angilletta and Sears wonder why extant birds and mammals are homeothermic endotherms rather than expressing endothermy only during the reproductive period. This question appears based on an inaccurate view of the extent to which mammals and birds are homeothermic. Although it was once thought that heterothermy in mammals was restricted to a few species living in cold climates, it is now known that heterothermy is common in orders containing approximately 75% of extant mammals. It is found in diverse taxa (including the phylogenetically basal groups) from all three subclasses of mammals and in diverse biogeographical settings ranging from the Arctic to the Tropics (Geiser 1998, 2003). Similarly, heterothermy in birds has been reported in species from 29 families representing 11 orders that range from tropical to arctic habitats and have body masses from <3 to 6,500 g. It is probably more widespread, but the majority of groups have not yet been studied. Heterothermia may be plesiomorphic for Aves, although more data will be needed to confirm this (McKechnie and Lovegrove 2002).

Heterothermy does not necessarily cause locomotor dysfunction or torpor, but many heterothermic animals are capable of torpor, especially small animals that feed on unpredictable food sources (nectarivores, aerial insectivores, frugivores; McNab 1986; McKechnie and Lovegrove 2002). Torpor may help match foraging efforts to cycles of food availability, and the fact that food often obviates torpor reinforces the idea that energy availability must be taken into account to understand the fitness costs of endothermy (Geiser 1988; Morris et al. 1994; Geiser and Ruf 1995; McKechnie and Lovegrove 2002). Endothermy is best suited to large animals in energy-rich environments and ectothermy to small animals in energy-poor environments (Pough 1980).

Although heterothermy is common among extant endotherms, it is avoided during reproduction both during embryo incubation and while brooding juveniles (Howell and Dawson 1954; Calder 1971; Vehrencamp 1982; Audet and Fenton 1988; Fowler 1988; Geiser 1988; Beard et al. 1992; Stephenson and Racey 1993; Hamilton and Barclay 1994; Poppit et al. 1994; Ancel et al. 1998; Geiser et al. 1998; McKechnie and Lovegrove 2002). When heterothermic animals allow or are forced through inadequate food supplies to decrease body temperature during reproduction, the reproduction period is extended and/or the reproductive effort is adversely effected (Audet and Fenton 1988; Brigham 1992; Kissner and Brigham 1993; Csada and Brigham 1994; Buffenstein et al. 1996). An important mechanism that reduces heterothermy during reproductive periods appears to be reproductive hormones. For

example, leptin and progesterone reduce torpor (Geiser et al. 1998; Feay et al. 2003). Thus the pattern of expression of homeothermy and heterothermy and their mechanisms of control in extant birds and mammals corroborates the reproductive scenario.

Sexual Differences

Angilletta and Sears are puzzled by the idea that endothermy in males can be explained by parental care. Biparental care is basal in birds and often includes embryo incubation by males. In contrast, monoparental care is basal and predominate in mammals (Reynolds et al. 2002). Yet we know there can be traits expressed in male mammals because of selection acting on reproductive characters in females. Consider the presence of nipples and mammary glands in males. Furthermore, adaptation to different thermal norms requires changes in multiple enzyme systems. The vast majority of genes are contained on autosomal chromosomes that are randomly inherited by male and female offspring alike, and the expression of the genes is not dependent on the parent of origin (with the rare exception of the imprinting genes). Thus in many cases, selection on females must shape the gene pool and the phenotype of males as well.

Comparison of the Plausibility of the Aerobic Capacity and Reproductive Models

Angilletta and Sears suggest that using the aerobic capacity model (Bennett and Ruben 1979) to explain the evolution of endothermy is more plausible than using the reproductive model. To compare the aerobic capacity and reproductive hypotheses, it is important to note that both models explain the correlation between endothermy and an expanded ability to sustain vigorous exercise, but the theories are distinct in the postulated polarity of these traits and the expected strength of the correlation. The reproductive model proposes high aerobic capacity evolved to expand a parent's ability to obtain resources to warm and feed offspring. Furthermore, other contributing factors such as food source and distribution, mode of locomotion (e.g., flight, terrestrial locomotion), intraspecific competition and displays, and predator-prey interactions were proposed to influence the evolution of aerobic capacities. Because of this complex intertwining of multiple factors, the reproductive model proposes that a large range of aerobic activity metabolisms could evolve among different lineages with similar basal metabolisms (Farmer 2000). In contrast, the aerobic capacity model (Bennett and Ruben, 1979) proposes that basal (standard) rates of oxygen consumption are constrained by a physiological linkage to coevolve with maximal rates of oxygen consumption (elic-

ited by exercise). Selection could not uncouple basal from maximal aerobic metabolism even though the increased basal metabolic rate initially carried a fitness cost but no fitness benefit. Importantly, this hypothesis predicts that changes in basal metabolism will always parallel changes in maximal aerobic metabolism (Bennett 1991; Hayes and Garland 1995). To normalize for body mass, comparisons have commonly been made using aerobic scopes, the ratio of the maximal ($\dot{V}O_{2\max}$) and basal (BMR) rates of oxygen consumption.

Insect Data

Flying insects have by far the highest mass-specific rates of aerobic metabolism in the animal kingdom (Suarez et al. 2000) but retain their low standard metabolic rates; insects have aerobic scopes 20-fold and more those of vertebrates. Somehow, insects circumvent the purported linkage of basal (standard) and activity metabolisms. Bennett and Ruben (1979) suggested that the tracheal respiratory and open circulatory systems of insects allow them to circumvent the constraint and that the vertebrate linkage mechanism resides in the cardiopulmonary system; however no cardiopulmonary linkage has been found yet. Thus Angilletta and Sears suggest the linkage mechanism involves the lipid composition of membranes. Furthermore, Angilletta and Sears imply there is a visceral linkage mechanism; that is, BMR is increased by the expanded demands placed on viscera to digest and assimilate the nutrients that are needed to support expanded aerobic capacity. Others have also explored a connection between BMR and aerobic capacity and/or daily energy expenditure (Kirkwood 1983; Karasov and Diamond 1985; Weiner 1989, 1992; Peterson et al. 1990; Konarzewski and Diamond 1994; Ricklefs et al. 1996; Burness et al. 1998; Koteja 2000). However, insects remain an important counterargument to these putative linkage mechanisms. Flying insects manage to digest, assimilate, and process even greater amounts of food to fuel their activity than is needed by vertebrates without elevating standard metabolism. The insects' digestive system is much more similar to vertebrates than the insects' respiratory and circulatory systems. Thus, Angilletta and Sears have left unanswered the question of how selection can uncouple the evolution of the enormously expanded aerobic capacities of insects (Suarez et al. 2000) from their standard metabolism, but these metabolisms are constrained to coevolve in vertebrates.

Vertebrate Data

Most data on basal and maximal rates of oxygen consumption fit the reproductive scenario better than the aerobic capacity model. For example, Hammond et al. (2000)

examined aerobic performance and organ and muscle mass in red jungle fowl. These birds do not engage in sustained flight, but males engage in sustained and vigorous fights and displays to compete for mating and social status. Furthermore, it has been shown that these birds have substantial and repeatable variation in aerobic capacity within each sex and a striking sexual dimorphism in aerobic capacity between sexes (Hammond et al. 2000). While males have significantly higher maximal aerobic capacities ($\dot{V}O_{2\max}$) than females, males also have significantly lower BMR. The aerobic scopes of males were found to be 97% higher than for females (13.1 and 6.6, respectively). The high aerobic capacity of males appears to place fewer demands on the digestive system than the tasks carried out by females. Compared with males, the intestinal tracts of females were 75% heavier, the livers were 51% heavier, and the reproductive organs were 350% heavier, while organs of oxygen uptake and transport (heart, lungs) were 43% heavier in males and leg muscles were 29% heavier in males. Total muscle mass was 16% heavier in males than females. These data do not support the idea that the basal metabolism of endotherms is explained by the demands placed on viscera by expanded aerobic capacities. Furthermore, the data demonstrate that selection can act to increase $\dot{V}O_{2\max}$ without increasing BMR. In contrast, these data support the reproductive hypothesis that suggests that aerobic activity metabolisms are a consequence of a large number of intertwining factors, for example, intraspecific fights and displays, foraging demands, and others.

Many other intraspecific studies do not find a positive correlation in BMR and $\dot{V}O_{2\max}$ (Chappell et al. 1999). When a positive correlation is found in a group, it is generally very weak, and there is no evidence that the correlation is due to causation (Hayes and Garland 1995). Nor do comparisons between species generally support the aerobic capacity model. For example, the aerobic capacity hypothesis predicts that animals with low basal metabolic rates, such as marsupials, will also have low maximal rates of oxygen consumption. Contrary to this prediction, many marsupials have very high maximal rates of oxygen consumption, giving them significantly greater aerobic scopes than many eutherians (Hinds et al. 1993). Similarly, only one of seven species of lizards examined showed a positive correlation between resting and maximal rates of oxygen consumption (Hayes and Garland 1995). Comparing among a broad range of mammalian species it appears that basal metabolism varies allometrically as a function of body mass raised to the exponent of 0.76; in contrast, $\dot{V}O_{2\max}$ varies as mass raised to the exponent of 0.87 (Hulbert and Else 2000). The difference in exponents means that small mammals have lower aerobic scopes than large mammals (Hulbert and Else 2000), a finding that is

counter to the aerobic capacity hypothesis. Furthermore, other predictions of the aerobic capacity hypothesis have not been supported by subsequent research (e.g., that aerobic scopes are fixed between values of 5–10); it is clear these scopes vary widely (Taylor et al. 1981; Bennett 1982; Weibel et al. 1987, 1992; Hinds et al. 1993; Hayes and Garland 1995; Thompson and Withers 1997; Farmer and Carrier 2000).

Angilletta and Sears suggest that there is evidence showing that increases in the level of activity of birds elevates the resting metabolic rate (RMR; Nilsson 2002). However, numerous other studies have shown the opposite effect. For example, in a study of white-crowned sparrows, implantation of testosterone significantly increased activity levels but decreased both diurnal and nocturnal resting metabolic rates (Wikelski et al. 1999). Similarly, testosterone implants increased activity but not daily energy expenditure in dark-eyed juncos, presumably due to a decrease in RMR (Lynn et al. 2000). In zebra finches, daily activity regimes (perch hopping) decreased both nocturnal metabolic rates (up to 12%) and resting metabolic rate during the inactive period of the day (approximately 38%; Deerenberg et al. 1998a, 1998b). Activity is also associated with a decrease in BMR in barnacle geese (Butler and Woakes 2001). Barnacle geese undergo a strenuous migration, 2,500–3,000 km in just a few days. Commencing several days before migration, continuing during the migration, and for about 20 d after the start of migration, their body temperature drops by about 4.4°C. This is thought to lower BMR by approximately 34%–39% (Butler and Woakes 2001). Looking broadly at many species of birds, high daily energy expenditures were not correlated with high basal metabolic rates (Ricklefs et al. 1996). As we can clearly see from insects and from birds, extraordinarily high levels of oxygen consumption and activity are possible without increases in basal rates of metabolism. Except in the broadest taxonomic sense that birds and mammals are generally more active than ectothermic tetrapods, high levels of activity are not always even associated with high BMR. On the contrary, these data on activity in birds show that high levels of activity can be correlated with and possibly even cause lowered BMR.

Birds do not appear exceptional in this regard. Increases in maximal aerobic capacities do not increase basal or resting metabolic rates in humans (Meredith et al. 1989; Frey-Hewitt et al. 1990; Meijer et al. 1991; Schulz et al. 1991; Broeder et al. 1992a, 1992b; Horton and Geissler 1994; Bullough et al. 1995; Wilmore et al. 1998). In rodents, selection for increased $\dot{V}O_{2\max}$ does not increase BMR (Konarzewski et al. 1997), selection for decreased BMR does not decrease $\dot{V}O_{2\max}$, and selection for increased BMR does not increase $\dot{V}O_{2\max}$ (Konarzewski et al. 2003).

Ultimately, the plausibility of a hypothesis needs to be

based on its fit to the data rather than its intuitive appeal. The aerobic capacity hypothesis is a very good idea and has stimulated a lot of research, but the data do not support it, and therefore other explanations should be sought for the correlation between endothermy and the expanded aerobic capacities of birds and mammals. It is plausible that the increased energetic burden of providing food and heat to offspring represented the original basis for selection of individuals with expanded aerobic activity capacity.

Mechanism

Angilletta and Sears suggest that the ratio of polyunsaturated lipids in cell membranes is a plausible mechanism for the aerobic capacity hypothesis because these lipids link cellular rates of oxygen consumption (RMR), thermoregulatory ability, growth rate, and the aerobic capacity of the organism ($\dot{V}O_{2\max}$). This idea is questionable because RMR peaks in the neonatal period, but $\dot{V}O_{2\max}$ is greatest in the adult (Chappell et al. 1999; Hulbert and Else 2000). Importantly, $\dot{V}O_{2\max}$ is determined by the integration of the organ systems of the oxygen cascade: the mass of the muscle performing the activity, the density of capillaries in the muscle, the rates of ventilation, the hematocrit, the cardiac output, the pulmonary diffusion capacity, ventilation-perfusion matching, and more. Increases in the metabolism of cells and organs that support growth do not confer greater $\dot{V}O_{2\max}$. For example, in rat liver the metabolic rate is 3.5-fold greater in the neonate than in the adult (Hulbert and Else 2000), but the liver is not important for oxygen transport, and so this heightened metabolism of the liver increases RMR but does not increase $\dot{V}O_{2\max}$. Furthermore, organs such as lungs that are important to $\dot{V}O_{2\max}$ do not necessarily mature in the neonatal period when RMR is maximal but often require many years to reach their full capacity to transport oxygen (Weibel 1984). Recall that $\dot{V}O_{2\max}$ is elicited by exercise and many neonatal mammals and birds cannot yet walk, fly, or even see to support activity. Although membrane lipids may link RMR to growth rates, $\dot{V}O_{2\max}$ is determined by a complex integration of the organs that transport oxygen from the air to the mitochondria and is negatively correlated with growth rates and RMR.

Unlike the aerobic capacity model where purported linkage mechanisms are tenuous at best, there is a very clear relationship between reproduction, basal metabolism, growth rates, body temperature set points, and parental care behaviors; they are manifestations of the hypothalamus-hypophysis axis (Farmer 2001). The body's central thermostat and central command for reproduction is the hypothalamus. The hypothalamus directly controls body temperature set points and acute thermoregulatory

responses (e.g., shivering, vasoconstriction; Nagashima et al. 2000). Importantly, the hypothalamus also controls basal metabolic rate directly, by stimulating heat production through brown adipose tissue (BAT), and indirectly (through the hypophysis), by mechanisms of nonshivering thermogenesis besides stimulation of BAT (Nagashima et al. 2000). The hypothalamus also integrates information about photoperiod, temperature, and appropriateness of nest sites and mates with internal information important to reproduction (e.g., appropriate levels of fat stores, etc.) and issues directions to the hypophysis to initiate and control both reproductive physiology and behaviors (including parental care) and to control aspects of the body that determine thermal conductance (the buildup and shedding of scales, hair, feathers; see references in Farmer 2001). Numerous hormones integrate the multiple roles of this axis.

Consider the role of leptin in the regulation of reproduction, body temperature set points, energy expenditure and food intake, growth, and metabolism. Leptin appears to be widespread among vertebrates (Yaghoubian et al. 2001). It has been best studied in mammals and is a signal that body fat stores are sufficient for growth (Spicer 2001) and for reproduction to commence (Magni et al. 2000). In mammals, leptin is synthesized in fat, in the ovaries, in the placenta, and in lactating mammary glands (Himms-Hagen 1999; Sagawa et al. 2002). Receptors for leptin are located in the hypothalamus as well as peripheral tissues (including reproductive structures; Magni et al. 2000; Spicer 2001). Leptin increases basal metabolic rates and heat production in several ways, including driving the hypothalamic-pituitary-thyroid axis to produce more thyroid hormone and inducing the expression of uncoupling proteins that increase the leakiness of mitochondria and reduce the efficiency of ATP production. Leptin also causes thermogenesis by stimulating lipolysis (Reidy and Weber 2002). Leptin injections in a marsupial inhibited torpor, increased the minimum body temperature of the daily cycle, and increased rates of oxygen consumption (Geiser et al. 1998). Similarly, lizards (*Sceloporous undulatus*) injected with leptin had body temperatures 0.6°C higher than controls, and females (but not males) showed a 2.5-fold increase in standard metabolism (Niewiarowski et al. 2000). This is nearly identical to the increase in metabolism (2.22-fold) known to occur naturally in gravid compared with nongravid female *S. undulatus* (Angilletta and Sears 1999). Recall that basal metabolic rates of some endotherms are five- to 10-fold those of a reptile (Bennett and Ruben 1979). Thus, the reproductive hormone leptin alone potentially could account for 25%–50% of the difference in basal metabolic rates (Niewiarowski et al. 2000).

Other hormones (e.g., thyroid hormones) have similar integrative functions on reproduction and basal (resting)

metabolism. Animals with low and high BMR tend to have low and high plasma levels of thyroid hormones, respectively. For example, naked mole rats have the lowest mass-specific metabolic rates among mammals and low rates of heat production. The level of free thyroid hormone (T_4) in the blood of naked mole rats is about an order of magnitude lower than for other mammals and is on par with the levels found in ectothermic tetrapods (Buffenstein et al. 2001). Similarly, shrews have high basal metabolic rates for their body mass and also have high levels of thyroid hormones (Tomasi 1984). For a discussion of the importance of thyroid hormones to reproduction, see Farmer 2000 and references therein. One may need to look no farther than the network of hormones that control reproduction, metabolism, parental care behaviors, their actions at their target tissues, and their integration by the hypothalamus to find a common focus for selection to act concurrently to expand parental care behaviors and to evolve endothermy.

The Importance of Integrating Historical and Mechanistic Data

Angilletta and Sears's objections to the reproductive hypothesis appear to arise primarily from a cost-benefit analysis that does not integrate historical and mechanistic data. They portray the energetic cost of endothermy as so enormous that almost any alternative evolutionary path would be far more probable. For example, Angilletta and Sears conclude that the enormous cost of endothermy would have made a shift in the thermal tolerance of embryos a more likely course of evolution than parental warming of offspring. However, this argument is questionable when historical data are integrated with the mechanistic determinants of the costs of endothermy.

Historical data on the large body size of archosaurs and synapsids indicate that the initial costs of endothermy were unlikely to have been enormous; it is only very small animals that bear immense thermoregulatory costs. Although it is a common perception among physiologists that endothermy evolved in rodent-sized animals (e.g., 30–40 g; Crompton et al. 1978; Hulbert and Else 1999), a synthesis of multiple lines of evidence (e.g., bone histology, respiratory turbinates, predatory prey ratios, etc.) suggests that endothermy evolved in Late Permian therapsids and in the ornithosuchian line of archosaurs (Olson 1959; de Ricqlès 1974; Bakker 1975; Bennett and Ruben 1986; Hillenius 1992, 1994; Padian et al. 2001; Rubidge and Sidor 2001). The therapsids weighed from 10 to 200 kg, with some as large as half a ton, and were heavy-bodied, large-headed, stumpy-legged forms (Pough et al. 1999). Similarly, non-avian dinosaurs were primarily medium to large animals; for example, the basal *Herrerasaurus* was 2.5 m long (Pa-

dian et al. 2001). In contrast, terrestrial nonarchosaurian reptiles primarily occupied a niche of small body size and continue to do so today; 80% of lizards weigh <20 g (Pough 1980; Pough et al. 1999), making endothermy a less probable evolutionary path in this lineage.

Concrete numbers of the costs of living in extant animals illustrate the importance of clearly distinguishing between the cost of evolving endothermy in the range of body sizes typical of lizards or in the range of body sizes of the actual archosaurian and synapsid lineages. For example, although on average 30-g mammals consume 16.0-fold more food each day than 30-g reptiles, 30-kg mammals need only 4.7-fold more food each day than 30-kg reptiles (Nagy 2001). These numbers are based on regression analyses of field metabolic rates (FMR) of 79 mammalian and 55 reptilian species. Importantly, because FMR includes the cost of activity, the cost of thermoregulation, and maintenance costs (e.g., basal metabolic rate, costs of digestion, costs of immune activity), the cost of thermoregulation and endothermy per se is a fraction of the FMR. Few studies have partitioned daily energy budgets into its components. However, the limited available data indicate that activity constitutes a sizable fraction of FMR. For example, for a small passerine bird (6.5 g) in winter (mean low and high temperatures: 6.8° and 25.9°C), activity constituted approximately 21.0% of the daily energy expenditure (DEE) while defense against cold was 19.5% of DEE. In summer, the costs of activity and thermoregulation were 17.5% and 10%, respectively (Webster and Weathers 2000). Activity is expected to constitute a more sizable fraction of the daily costs in larger animals. A study of sedentary humans (65.8 kg) in which subjects were not permitted volitional exercise (sports or fitness-related activity) found the costs of nonexercise activity (maintenance of posture, fidgeting, and other physical activities of daily life) and digestion to constitute about 40% of the total daily energy expenditure (Levine et al. 1999). More active animals spend more of their daily budget on activity. For example, African wild dogs (25 kg) expend approximately 60% of the energy needed each day in the 3.5 h/d that they hunt (Gorman et al. 1998). Thus, in medium-sized extant animals (e.g., 30 kg), exercise and digestion constitute roughly 40%–60% and more of the daily costs of living, and the energetic cost of supporting endothermy per se (BMR and costs of thermoregulation) is approximately only two- to threefold the FMR of ectotherms with the same mass.

The cost of endothermy is also determined by body shape. Angilletta and Sears suggest pythons are a perfect model for how evolution would have unfolded in archosaurs and synapsids if thermogenesis had evolved due to selection for embryo incubation, but long thin animals have unfavorable body forms for endothermy (Pough

1980). For example, mustelids have large surface area to body mass ratios and basal metabolic rates up to six times greater than nonelongate mammals of equivalent mass. Therefore, they have high food requirements; least weasels consume 30%–40% of their weight in food each day (reviewed in Zielinski 2000). Considering that mustelids are not nearly so long and thin as snakes, it becomes clear that, except when python bodies are curled into balls around their nests of eggs, the extremely elongate shape of pythons would cause them to incur very high energetic cost for homeothermic endothermy. Furthermore, the body forms of the early synapsids and archosaurs that evolved endothermy were not shaped anything like a snake. Thus pythons are a poor model for the evolution of endothermy in these lineages.

Besides considering appropriate body masses and shapes, a realistic analysis of the initial energetic costs of producing heat for offspring should consider both thermal conductance and the temperature gradient requisite to affect reproduction. It is logical to consider that insulation, in the form of a nest or burrow, was present with the evolution of thermogenesis. We know that female pythons push leaf litter into mounds to form nests (Slip and Shine 1988) and seek out sheltered sites, for example, abandoned burrows of varanid lizards, root boles (Shine et al. 1997b). Furthermore, the first endotherms need not have supported the large temperature gradients found in extant eutherian mammals. Data on development in reptiles show that increases in temperature of only several degrees can have significant effects on embryos and juveniles and that pythons elevate nest temperature 13°C. Thus, neontological data show that relatively small temperature gradients (2°–13°C) are affordable and affect reproduction.

Finally, the mechanism of thermogenesis should be considered. In the reproductive model, the initial mechanism of nonshivering thermogenesis is proposed to have been the elevated metabolism known to occur with reproduction in both ectothermic and endothermic vertebrates (Guillette 1982; Birchard et al. 1983; Thompson and Nicoll 1986; Prentice and Whitehead 1987; Forsum et al. 1988; Thompson 1992; Angilletta and Sears 1999; Butte et al. 1999; Hsu et al. 1999; Robert and Thompson 2000; Antinuchi and Busch 2001; Johnson and Speakman 2001). Reproduction is a time of synthesis and heat is a by-product. For example, the large increase in resting metabolic rate of lactating mammals (reviewed in Hammond and Diamond 1997) serves both to produce milk and to warm young. Thus part of the thermogenesis cannot be considered simply an additional cost because it is an integral aspect of reproduction. The reproductive hypothesis is further corroborated by the fact that in extant animals, differences in individual basal metabolic rates exist that are significant and consistent (Bech et al.

1999; Hammond et al. 2000). Thus it is plausible that individuals with higher metabolisms and better thermogenic abilities could have raised the temperature of their offspring and had greater reproductive success than their conspecifics.

Summary

The adaptive significance of endothermy is a fascinating question to many biologists interested in vertebrate evolution. Traditionally, the selective factors leading to the evolution of endothermy have primarily been related to locomotor performance, while the energy used for thermogenesis has been viewed as energy that otherwise could have been allocated to growth and reproduction (Bennett and Ruben 1979). In marked contrast, the reproductive hypothesis proposes that the primary benefits of endothermy are reproductive (occurring to growing embryos and juveniles), while thermogenesis represents an increase in the rate and amount of energy invested into reproduction. Thermogenesis is suggested to have functioned to speed and facilitate development and growth of embryos and juveniles. Both thermogenesis and parental feeding of young greatly expanded the energetic needs of the archosaurian and synapsid lineages. It is this expanded energetic investment into reproduction that may have represented the original basis for subsequent selection of individuals with expanded aerobic activity capacities. Thus, great aerobic capacity may correlate broadly with tetrapod endothermy because both traits are adaptations arising from reproductive selective pressures. A strong line of evidence supportive of the reproductive hypothesis is the convergent evolution of thermogenesis as an adaptation for reproduction in multiple lineages of insects, multiple lineages of plants, protists, and reptiles.

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